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Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: a case study of the wolf in Switzerland

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Running title: A socio-ecological framework to map wolf distribution

Summary

1. Habitat suitability models are commonly used in conservation practice to assess the potential of an area to be occupied and colonised. A major limitation of these models, however, is the omission of spatially explicit understanding of human acceptance towards the focal species. As wildlife is more and more subject to human-dominated landscapes, ignoring the sociological component will result in misrepresentation of the observed processes and inappropriate management.

2. We distributed 10 000 questionnaires across Switzerland and identified key socio-demographic factors correlated with human acceptance of the wolf. We then created a spatially explicit acceptance model based on geo-referenced socio-demographic, social and geographic information. Finally, we combined our acceptance model with a habitat suitability model to obtain a unified socio-ecological suitability model, which included human and ecological components.

3. We showed that the key factors associated with human acceptance were perception of how harmful the wolf is, interest in wolf-related issues, need for livestock protection, and fear of the wolf. Perceived harmfulness was in turn correlated with direct and indirect experience with the wolf, and level of education.

4. Our acceptance map predicted decreasing acceptance with increasing altitude of residency and proximity to locations of confirmed wolf presence. This resulted in overall opposition to the wolf for the Alpine region, albeit substantial regional differences.

5. We found little spatial overlap (6% of Switzerland) between areas where the wolf was accepted and areas of suitable habitat. These areas of socio-ecological suitability were concentrated in the Jura Mountains and in the eastern and southern Alps, and were absent in the western and central Alps. Particularly in the Jura region, which is yet to be colonised, management of human acceptance will be a crucial conservation target.

6. *Synthesis and applications.* We developed an integrative, socio-ecological approach that allowed us to accurately reproduce recent wolf recolonisation. We anticipate our framework to be a powerful tool to reliably evaluate overall suitable habitats and predict short-to-medium-term range expansion for species whose distribution is also dependent on human attitudes. Because our approach is sensitive to both the ecological and human component, it is ideally suited to identify key regions where proactive and targeted socio-ecological management plans are needed.

Key-words: *Canis lupus*, conservation, habitat suitability model, human-wildlife conflict, range expansion, recolonisation, large carnivores, socio-demographic factors, sociological survey

Introduction

Large carnivores are declining worldwide as a consequence of human-induced habitat loss and degradation, a declining prey base, and direct anthropogenic persecution (Sanderson *et al.* 2002; Treves & Karanth 2003; Ripple *et al.* 2014). Under these scenarios, several models have been developed to understand and predict animals' distribution and characterise suitable areas (Boyce & McDonald 1999; Hirzel *et al.* 2002; Schadt *et al.* 2002a; Guisan & Thuiller 2005; Boyce *et al.* 2015). These habitat suitability models (HSMs) typically use observed animal locations (e.g. sightings) and ecological characteristics (e.g. vegetation type) at and around these locations to infer preferred and suitable habitats (Engler, Guisan & Rechsteiner 2004; Gu & Swihart 2004; Falcucci *et al.* 2009). However, a major limitation of HSMs is the omission of spatially explicit information on the human dimension. This omission can have severe consequences, particularly for large carnivores that often suffer from a negative reputation and direct persecution due to conflict with humans. Excluding the human dimension from HSMs would mean, for example, that a suitable habitat patch in a wildlife-friendly human landscape has the same occupancy potential as a similar suitable patch in a wildlife-hostile landscape.

The human dimension is particularly important for species that encroach into human-dominated landscapes as a consequence of recolonisation and range expansion, giving rise to complex interactions between environmental and anthropogenic factors. For example, recolonisation by large carnivores is likely to be opposed in landscapes dominated by people whose understanding of nature no longer includes the focal species as an integral component. Such unfamiliarity can lead to fear and intolerance due to inability to relate to the presence of an apparently novel component in an idealised version of nature (Kellert *et al.* 1996; Dickman 2010; Chapron *et al.* 2014). Negative attitudes may translate into lobbying and a hostile political microclimate, obstruction to wildlife management plans, or retaliatory killing

(Linnell, Swenson & Anderson 2001; Treves *et al*. 2014). Positive public attitudes are generally expected in areas where carnivores are absent or where they have always coexisted alongside with people (Kellert *et al*. 1996; Kaczensky, Blazic & Gossow 2004; Majić & Bath 2010). Because human attitude is a crucial factor shaping animals' distribution and habitat use, and influencing long-term persistence of local populations (Mech 1995; Mech & Boitani 2003; Dickman 2010; Chapron *et al*. 2014), its inclusion in HSMs is key to increase model predictive power. This allows a more reliable assessment of occupancy and evaluation of recolonisation potential, and thus the implementation of sound evidence-based actions.

During the past century, large carnivores have been heavily persecuted and locally extirpated throughout continental Europe (Ripple *et al*. 2014). In Switzerland, wolves (*Canis lupus*) were completely eradicated by the end of the 19th century due to persecution following expansion of human settlements, loss of livestock, and competition with humans for game species (Breitenmoser 1998). By the beginning of the 20th century, across the entire Alpine range, isolated wolf populations persisted only in Italy and in the Balkans (Ciucci *et al*. 2009). As a result of legal protection, during the last decades, the Italian wolf population increased in size and expanded its range from the Apennines to the Western Alps (Valière *et al*. 2003; Fabbri *et al*. 2007; Marucco *et al*. 2009). The first 'Italian wolf' reached Switzerland in 1995, after over a century of absence from the Swiss territory (Glenz *et al*. 2001), generating turmoil and strong negative reactions particularly among rural communities (Hunziker, Hoffmann & Wild-Eck 2001; Wallner & Hunziker 2001).

Today, Switzerland is characterised by vast areas of favourable wolf habitats, which include areas with low human density, intermediate elevations, high prey richness, and the presence of natural land covers (Glenz *et al*. 2001; Marucco & McIntire 2010; Falcucci *et al*. 2013). Under similar favourable natural conditions, the formation of stable and reproducing packs is typically observed 2–7 years after first recolonisation by single long-distance dispersers (Poulle, Lequette & Dahier 1999; Wagner *et al.* 2012; Fabbri *et al.* 2014) with subsequent population expansion. For example, first wolves were observed in France in 1992 and by 2003 the wolf population in the French Alps was estimated to be >120 individuals (Cubaynes *et al.* 2010). Similarly, wolves were first reported in Germany in 1998 and 16 years later, 25 packs lived in the eastern region of the country (Reinhardt *et al.* 2015). Such rapid expansion and increase in numbers are reported also for North America, and are the result of the species' long-distance dispersal ability and reproductive success (Mech, Fritts & Wagner 1995; Boyd & Pletscher 1999; Vilà *et al.* 2003). Despite the prevailing favourable ecological conditions in Switzerland, however, 20 years after the first observed recolonisation event only a handful of single wolves and one pack live in the country (KORA, unpublished data). The recolonisation process of the Swiss territory appears notably slow compared to similar regions in Central Europe. We speculate that the slow recovery of the wolf in Switzerland is largely due to a low level of acceptance and legal and illegal persecution that outweigh the favourable ecological conditions. At least 15 wolves died of unnatural causes between 1998 and 2015; three were poached, eight were legally shot by the authorities due to conflict with livestock farming, and four were train / road kills (Table 1). This is a remarkable number given the small wolf population size.

The aim of this study was to integrate both the human and the ecological dimensions in a unified framework to better assess suitable wolf habitats in Switzerland and better understand expansion and recolonisation processes. We first investigated the socio-demographic factors related to human acceptance of the wolf. For this purpose, we sent 10'000 questionnaires across all geographic regions in Switzerland. Based on the responses to our questionnaires, we created a spatially explicit model of human acceptance. Finally, we combined our human acceptance model (HAM) with an HSM to create a final socio-ecological suitability model (SESM) that included both human acceptance and ecological components.

Materials and methods

Study Area

This study was conducted across Switzerland, spanning an area of 41’285 km^2, during 2015. Cultivated areas, pastures, forests, grasslands, bare soil, and rocks on mountain slopes as well as human infrastructure characterise the Swiss landscape. Three distinct topographic regions can be recognised: The Alpine region in the south (max. elevation 4634 m above sea level), the densely populated Central Plateau in the middle, and the Jura Mountains in the north (max. elevation 1720 m above sea level). The Alpine region is in turn divided in western, central, eastern and southern Alps (Fig. 1). Switzerland’s administration is divided into 26 cantons, which to some extent represent regional, social and cultural differences.

Questionnaire sampling

For targeting our questionnaires, we sampled 10’000 random locations across Switzerland. We assigned to each random location the postcode of the closest settlement (i.e. village, town, or city). Several random locations were assigned to the same settlement; in total 2580 (63%) settlements were sampled from a total of 4070 Swiss settlements. Those random locations (e.g. on mountain peaks) that were >5 km from the closest settlement were again randomly redistributed within the same topographic region. The choice of the 5 km threshold was based on the radius of human perception of the spatial environment (Schirpke, Tasser & Tappeiner 2013). This sampling procedure ensured spatially representative sampling of interviewees, as opposed to a density-based sampling method, which would have resulted in oversampling of larger cities.

For each random location / settlement, we randomly selected private households using the official phonebook of Switzerland. To allow for random sampling of age and gender within a household, we requested the adult (≥16 years old) who was born earliest in the annual calendar to fill the questionnaire (Hunziker, Hoffmann & Wild-Eck 2001). We sent questionnaires by mail in the language of the respective region along with a pre-paid envelope for return consignment. Interviewees had the option to answer either by mail or to fill the questionnaire online; both responses were anonymous. A total of 9428 questionnaires were successfully delivered (in some cases the recipient had moved or died, or the address was incomplete) and we received back 3142 filled questionnaires (33.3%), corresponding to 1757 settlements. Only 5% of the interviewees used the online questionnaire.

Questionnaire design and correlates of human acceptance

We scored human acceptance based on six questions (questions A1-A6; for the English version of the questionnaire see Appendix S1 in Supporting Information). To evaluate correlates of acceptance, we used models of social acceptance and public attitudes towards carnivores (Wallner & Hunziker 2001; Kaczensky, Blazic & Gossow 2004). Accordingly, we included socio-demographic parameters (e.g. gender, age, education) and eight factors (*knowledge* of the wolf, *interest* in wolf-related issues, *fear* of the wolf, perceived *harmfulness* of the wolf, perceived *spatial proximity* of the wolf, *direct experience* with the wolf, *indirect experience* with the wolf, and need for *livestock protection*) in our a priori model (see Appendix S1 for a detailed description of the eight factors). Following Hunziker, Hoffmann & Wild-Eck (2001), Bruskotter, Schmidt & Teel (2007), and Kaczensky, Blazic & Gossow (2004), we formulated 2-6 questions for each factor (Appendix S1). Responses were either measured on a five-point Likert scale (Likert 1932) or as multiple-choice answers. We calculated a mean score for each factor assessing the answers to the corresponding questions (Appendix S2).

To assess internal consistency among the answers to the questions representing each factor (Kaczensky, Blazic & Gossow 2004), we calculated the reliability coefficient

Cronbach's alpha (α) (Zeller & Carmines 1980). Alpha values suggested inconsistency ($\alpha<0.7$) for *direct experience*, *indirect experience*, and *knowledge* (Appendix S2). We therefore used principal component analysis (PCA) to re-group the questions (G1, G2, G3, H1, H2, D1, D2, D3, D4) of these three factors as suggested by Hunziker, Hoffmann & Wild-Eck (2001). Five questions (D1, D2, D3, D4, G1) could not be grouped and were dropped. The other questions (G2, G3, H1, H2) formed one new group (factor) that we named *experience* with the wolf.

Finally, we performed multiple linear regression analysis to assess the relationship between level of acceptance and the socio-demographic parameters and six remaining factors. Since the factor *harmfulness* was highly correlated with other explanatory variables, we additionally performed linear regression analysis with *harmfulness* as dependent variable. We standardised input variables (Gelman 2008) and selected a single best model from all candidate models based on Akaike's Information Criterion (AIC) (Burnham & Anderson 2002). We performed all statistical and spatial analyses in R (R Core Team 2015).

Modelling spatial distribution of human acceptance

We used the first question of the questionnaire "Are you in favour or against wild living wolves in Switzerland?" to determine human acceptance. Possible answers with assigned levels of acceptance (*LoA*) were: in favour (1), somewhat in favour (0.75), neither nor (0.5), somewhat against (0.25) and against (0). Because some settlements were sampled multiple times (i.e. more than one questionnaire was sent to the same settlement), we calculated a mean level of acceptance for each settlement. We used settlement-specific *LoA* values as the response variable in a logistic regression analysis for proportional data (Guisan, Edwards & Hastie 2002; Zuur *et al*. 2009). We used geo-referenced demographic, social and geographic parameters to create a spatially explicit human acceptance model (HAM) for the entire study area. After accounting for collinearities, the final set of geo-referenced predictors used in the full model were: *human density*, *mean age*, *language*, *tourism intensity*, *small livestock* (sheep and goat abundance), *wolf distance* (distance to nearest location of confirmed wolf presence), *depredation* (number of depredated small livestock), *elevation*, and *agricultural areas* (Appendix S3). We did not use *human-related wolf mortality* as predictor due to the methodological inconvenience of including very few and spatially distinct data points on a nationwide, large-scale analysis. Each predictor was represented as a raster layer with a resolution of 100 m x 100 m (Fig. 2). For each predictor, we calculated the value of each raster cell using a focal function applied over a circular moving window of 5 km radius. For example, the *human density* value of a given raster cell was the sum of the number of people living within a 5 km radius (Appendix S3). Since the response variable displayed spatial autocorrelation (i.e. settlements close to each other exhibited more similar *human acceptance* values than those further apart), we included an autocorrelation covariate (hereafter: autocovariate) as an additional predictor in the final model (Dormann *et al*. 2007). We calculated the autocovariate as distance weighted-sum of neighbouring response values (Bardos, Guillera-Arroita & Wintle 2015). We standardised predictors (Gelman 2008) and followed a backward selection procedure based on AIC (Burnham & Anderson 2002) to simplify the full model, which also included two-way interactions.

We evaluated the predictive performance of our HAM on the basis of the area under the receiver operating characteristic curve (AUC) following 10-fold cross-validation (Elith & Leathwick 2009). AUC measures the overall performance of a model; a model that does not perform better than chance has an AUC of 0.5. We then applied the final model to the entire dataset to predict the probability P_{HAM} associated to each raster cell. The higher the values of P_{HAM} the higher the level of acceptance. Raster cells further than 5 km from any settlement (e.g. mountain peaks) were not assigned a P_{HAM} value (Fig. 3A).

Creation of a socio-ecological suitability model

We combined our human acceptance model (HAM) with a habitat suitability model (HSM) developed by Falcucci *et al*. (2013) to create a final socio-ecological suitability model (SESM). Falcucci *et al*. (2013) used wolf presence data obtained from the Italian and French Alps, and considered environmental (e.g. land cover), abiotic (e.g. topography) and anthropogenic (e.g. distance to infrastructure) factors to produce a model of the potential distribution of the wolf over the Alpine range. Similar to our HAM, the HSM by Falcucci *et al*. (2013) assigned a continuous suitability value (for clarity renamed P_{HSM}) to each pixel within the entire study area (Fig. 3B). High P_{HSM} values represented highly suitable areas and low P_{HSM} values represented unsuitable areas. Because P_{HAM} and P_{HSM} values are not directly comparable in terms of realised suitability (in other words, a pixel with P_{HAM}=0 and P_{HSM}=1 is not necessarily equally as suitable as a pixel with P_{HAM}=1 and P_{HSM}=0), they cannot be multiplied to obtain continuous P_{SESM} values. We therefore transformed the continuous P values of both models to a binary outcome (Figs 3C & 3D) – acceptance vs. opposition (for the HAM) and suitable vs. non suitable (for the HSM) – by setting a model-specific threshold t (Elith & Leathwick 2009). For the HAM, the mean threshold obtained from 10-fold cross-validation at which the sum of the sensitivity (true positive rate) and specificity (true negative rate) was highest was t=0.47. Predicted P_{HAM} values above this threshold were classified as acceptance of the wolf and values below as opposition to the wolf (Fig. 3C). We obtained threshold values for the HSM from Falcucci *et al*. (2013). We considered intersection between areas where the wolf was accepted ($HAM_{acceptance}$) and areas characterised by a suitable habitat ($HSM_{suitable}$) as overall suitable in our final socio-ecological suitability model (SESM) (Fig. 3E):

$$SESM_{suitable} = HAM_{acceptance} \cap HSM_{suitable}$$

Finally, we evaluated $SESM_{suitable}$ patches for their potential to sustain wolves based on two criteria (Schadt *et al*. 2002b). Patches were retained and considered overall suitable, either if (1) their area was ≥23 km^2, which corresponds to wolves' core areas in central Europe (Ciucci *et al*. 1997; Okarma *et al*. 1998; Kusak, Skrbinšek & Huber 2005; Schmidt, Theuerkauf & Kowalczyk 2007), or if (2) they were ≤ 20 km from a patch ≥23 km^2. This distance corresponds to the daily average distance moved by wolves in central Europe (Ciucci *et al*. 1997; Jędrzejewski *et al*. 2001; Kusak, Skrbinšek & Huber 2005).

To evaluate the potential effect of future changes in levels of acceptance on our SESM, we simulated two alternative scenarios. We changed the response of neutral interviewees, from neutral (*LoA*=0.5) to somewhat in favour (*LoA*=0.75), and from neutral to somewhat against (*LoA*=0.25). We then created two alternative SESM (Fig. S1) following the steps outlined above.

Results

Correlates of human acceptance

Our survey revealed an overall polarised but balanced opinion towards the wolf; 49% of the interviewees were against, 45% were in favour and 6% were neutral. After correcting for human density (note that we intentionally sampled by surface area and not by population density to obtain a representative spatial sampling of interviewees), however, the majority of the Swiss population (59%) was in favour of the wolf while only 34% were against it.

Appreciation of the need for livestock protection and interest in wolf-related issues (factors *interest* and *livestock protection*) were associated with high levels of acceptance of the wolf. On the other side, perception of the wolf as a harmful species and fear towards it (factors *harmfulness* and *fear*) showed a negative relationship with acceptance (Table 2). These four key factors alone explained 78% of the variation in acceptance scores, compared to the 79% of the fully parameterised model that also included perceived *spatial proximity* of the wolf and socio-demographic variables. Older people, men, livestock owners, hunters, and people with only basic education had an overall low level of acceptance; however, the total effect size of these variables was moderate compared to the four above-mentioned key factors (Table 2).

The main driver of *human acceptance* – perceived *harmfulness* of the wolf – was mainly associated with direct and indirect *experience* with the wolf, level of education, membership of an environmental NGO, and hunting activity of a person (Table S1). A negative *experience* and the interviewee being a hunter showed a positive relationship with the perception of the wolf as harmful. Interviewees with a university degree and a pro-environmental orientation, on the other hand, perceived the wolf as beneficial.

Spatial distribution of human acceptance

According to our spatially explicit model, acceptance of the wolf decreased with increasing *mean elevation* and increased with increasing *wolf distance* and *human density* (Table 3). In other words, our model predicted that people living at higher elevations were opposed to the wolf, and people living in densely populated areas or far from locations of confirmed wolf presence were in favour of the wolf. The interactive effect of *mean elevation* and *small livestock* resulted in low levels of acceptance for the wolf at higher elevation for regions characterised by a high abundance of sheep and goats.

In general, we predicted acceptance of the wolf for the Central Plateau ($\bar{P}_{HAM}$=0.73) and Jura Mountains ($\bar{P}_{HAM}$=0.59) while the Alpine region ($\bar{P}_{HAM}$=0.42) showed an overall opposition to the wolf (Figs 3A & 3C) albeit with substantial regional differences (Fig. 3A). Predictions of the cantons of Ticino ($\bar{P}_{HAM}$=0.47) and Graubünden ($\bar{P}_{HAM}$=0.44) in the southern and eastern Alps, respectively, were above average. The cantons of Uri ($\bar{P}_{HAM}$=0.36) and Valais ($\bar{P}_{HAM}$=0.34) in the central and western Alps, respectively, showed below average values. In terms of predictive performance, our HAM can be regarded as reasonably good (AUC=0.69).

Socio-ecological suitability model

Our socio-ecological suitability model, which considered both human acceptance and suitable habitats, returned a total of 68 patches (totalling 2567 km^2; i.e. 6% of Switzerland's area) characterised by acceptance of the wolf and favourable ecological conditions. 841 km^2 (33%) were located in the Jura Mountains, 1464 km^2 (57%) in the Alps, and the remaining 262 km^2 (10%) in the Central Plateau. This means that only 6% of the entire Alpine region was defined as overall suitable, as opposed to 19% of the Jura Mountains. Despite the favourable ecological conditions (Figs 3B & 3D), our socio-ecological suitability model did not predict any suitable patches for the western Alps and for most of the central Alps (Fig. 3E). For comparison, the habitat suitability model developed by Falcucci *et al*. (2013) predicted 944 km^2 (22%) of suitable habitat in the Jura Mountains and 12'948 km^2 (51%) in the Swiss Alps.

Our simulations showed that under the first scenario (i.e. neutral interviewees changed towards somewhat in favour of the wolf), the overall suitable habitat increased by 714 km^2 (+28%); while under the second scenario (i.e. neutral interviewees changed towards somewhat against the wolf) it decreased by 1526 km^2 (-59%). The difference in overall suitable area between the two scenarios (2240 km^2) corresponded to an area almost as large as the overall suitable area predicted under present conditions (Fig. S1).

Discussion

We integrated human acceptance and ecological components in a unified framework to better assess suitable wolf habitats in Switzerland. Our results suggested that this integrative approach more precisely represented – at least in the short to medium term – the wolf recolonisation potential and distribution in Switzerland compared to a model that only considered ecological variables. Specifically, the HSM by Falcucci *et al.* (2013) predicted vast suitable areas evenly distributed across the Swiss Alps (12’948 suitable km^2). However, despite 20 years of presence in the territory and high dispersal and recolonisation potential, the vast majority of suitable wolf habitat predicted by HSM has not yet been occupied. It appears that HSM for the wolf in Switzerland has a limited recolonisation predictive power. Our SESM was drastically more conservative (1464 suitable km^2) and better described regional differences. The human dimension captured in this study may indeed be more important than environmental variables for predicting wolf recolonisation and expansion in human dominated landscapes (Linnell, Swenson & Anderson 2001; Treves & Karanth 2003). This should not come as a surprise given the species’ ability to adapt to a variety of different environments (Llaneza, López-Bao & Sazatornil 2012) and the constant persecution it faces (Treves & Karanth 2003). Because our approach is sensitive to both ecological and human component, it represents a powerful tool to identify key regions where proactive and targeted socio-ecological management plans need to be enforced. Including the human component is especially important for sensitive political issues that receive wide social attention, such as the recolonisation of human-dominated landscapes by carnivore species.

The lack of suitable areas predicted by our SESM for the western Alps and for most of the central Alps was mainly driven by a widespread low level of acceptance rather than by the absence of suitable habitats. Interestingly, 20 years after first wolf appearance the western Alps have not yet been occupied by resident wolves. This is even more remarkable considering the vicinity to the well-established wolf population in France and Italy and considering that the western Alps represent the historical and geographic main immigration path to Switzerland (Fig. 1). On the other side, the higher level of acceptance of the wolf in the eastern and southern Alps resulted in vast areas of overall suitable habitat. Here, the presence of pups was confirmed in the cantons of Graubünden (in 2012 and following years) and Ticino (in 2015), 11 and 14 years after first wolf sighting in the respective cantons (KORA, unpublished data).

According to our SESM, the Jura Mountains in the north-western part of the country may represent a second wolf expansion zone, largely due to overall acceptance and suitable habitat. It is, however, worth noting that this predicted acceptance is largely influenced by distance from locations of confirmed wolf presence (the Jura region has only very recently been in contact with wolves; Fig. 1). Whether or not the present level of acceptance will change as wolves cross the unfavourable highly populated Central Plateau and expand across the Jura Mountains will largely depend on people's attitudes but also on public initiatives to influence acceptance and promote coexistence (Zimmermann, Wabakken & Dötterer 2001; Majić & Bath 2010; Treves, Naughton-Treves & Shelley 2013). In this regard, our integrative approach has the advantage of identifying zones of potential future conflict, thus allowing the development of site-specific management plans to increase level of human acceptance. The important role of the human dimension on overall habitat suitability is well illustrated by our simulations, where we showed that even changes in levels of acceptance in a small proportion of the population (6% of the interviewees) resulted in a substantial change in overall suitable habitat.

Our HAM confirmed the contrasting attitudes of the rural and urban population to wolf related issues (Kellert *et al.* 1996). Our results suggest that such contrasting opinions were linked to deep cultural and social differences and to contrasting livestock farming activities across different areas and altitudinal gradient (e.g. traditional pastoralism in remote areas vs. intensive, commercial husbandry activities at lower altitudes). We could not find any systematic information at the desired spatial scale about small livestock husbandry practices and we could therefore not investigate the topic in further detail. As attitudes are dynamic and evolving, and given the underlying social and cultural differences that shape them, proactive and targeted education schemes and awareness campaigns need be tailored to specific conditions and recipients. The effectiveness of such intervention should be regularly evaluated, for example through repeated surveys in order to monitor changes of acceptance over time. Unexpectedly, wolf depredation on livestock was not retained in our final HAM. We believe that this was due to the nature of the data, which is very much spatially and temporally clumped compared to the large spatial scale of the study (Fig. 2), rather than to a real lack of explanatory power. In fact, despite representing a negligible percentage across all Switzerland, depredation was higher in the western Alps (Table S2).

Low levels of acceptance were mainly driven by perception of the wolf as a harmful species, by fear towards the wolf, and by direct or indirect negative experiences. Similar results were found in a study conducted in the French Alps (Bath 2000). These findings thus highlight three key elements that should be considered if a higher level of acceptance has to be maintained or restored, as in the case of the Jura Mountains and eastern Alps, respectively. The belief that the wolf is dangerous to people (47% of interviewees), that it mainly feeds on livestock and not on wild ungulates (33% of interviewees), and that it would not avoid a person upon encounter (22% of interviewees) contributed to the general opposition to the wolf and showed the urgent need to address the “fear factor” through public education and objective information campaigns. A recent review has highlighted four major avenues of interventions to reduce people’s fear of large carnivores and change negative perceptions (Johansson *et al*. 2016). The overall negative connotations linked to the wolf may also largely be associated to media coverage only reporting of livestock depredation events or of alarming scenarios (Treves, Naughton-Treves & Shelley 2013; Fernández-Gil *et al*. 2016). In contrast, information about the positive effects of wolves on prey species or entire ecosystems (e.g. Ripple *et al*. 2001) are only rarely acknowledged and disseminated in Switzerland. According to expectations, perceived spatial proximity to wolves had a negative impact on acceptance (Karlsson & Sjöström 2007), yet this effect was much smaller than the effect size of perceived harmfulness and fear. In accordance to other studies, older people were more opposed to the wolf than younger people (Kellert *et al*. 1996; Wallner & Hunziker 2001). This difference may represent genuine generational differences and / or may indicate that young people develop negative attitudes over time. According to expectations, livestock owners, hunters, and people with basic education expressed opposition to the wolf. This confirms how the perception that the wolf has a negative influence on interviewees' personal activities (i.e. harmfulness factor) shapes attitudes (Kellert *et al*. 1996; Ericsson & Heberlein 2003). After correcting for human density, the overall acceptance of the wolf found in our study (59%) was in accordance with results from a study by Hunziker, Hoffmann & Wild-Eck (2001), who reported 61% positive attitudes for Switzerland. Because younger age classes were under-represented in our sample, our figure appears conservative.

Inferences based on our SESM were centred on the assumption that a low level of acceptance was directly linked to persecution (e.g. shooting), which delays wolf expansion, recolonisation, and settlement. This assumption seemed to hold for the present situation in Switzerland. In the western Alps, where our model predicted the strongest opposition to the wolf, eight wolves were shot (and additional five shooting licenses were granted) between 1998 and 2015 (Table 1), mainly due to predation on livestock. Despite the favourable environmental conditions (Falcucci *et al*. 2013), shooting wolves at a rate of one individual every 2.2 years, may have exacerbated Allee effect (Hurford, Hebblewhite & Lewis 2006) and prevented wolves from settling and reproducing. In contrast, only one wolf was shot in the eastern Alps during the 11 years between first sighting and first reproduction (Table 1). While it appears that shooting prevents (or at least delays) establishment and thus may reduce conflict in the short term, non-lethal methods have been shown more effective in preventing damage to livestock (Treves, Krofel & McManus 2016) and can lead to considerable changes in attitudes over a short time period (Majić & Bath 2010). On the other hand, beside sending a negative message, legal shooting may encourage poaching as it justifies the use of lethal methods (Chapron & Treves 2016). We advocate that only through implementation of management measures that promote the development of positive attitudes and enhance acceptance, governments can achieve a long lasting coexistence between people and wolves (Carter & Linnell 2016).

In summary, we showed that integrating human attitudes and habitat suitability in a unified socio-ecological suitability model (SESM) reduces predicted suitable area and helps better explain short to medium term distribution and patterns of recolonisation by the wolf. The remarkable difference in predicted suitable areas returned by the HSM and the SESM was, however, probably partly due to our integrative approach that discretised both HSM (suitable vs. non suitable) and HAM (acceptance vs. opposition) instead of using continuous raster values. Future work should identify techniques to precisely weigh HSM and HAM raster values to allow a more rigorous integrative approach. Habitat suitability models are commonly used in conservation practice; hence, their accuracy is crucial for the implementation of sound, evidence-based plans. In light of our findings, we anticipate suitability models for large carnivores to be revisited to include a spatially explicit human component, within the framework presented in this study. We believe that socio-ecological suitability models will become a powerful tool to assess suitable habitats for large carnivores, but also for other species whose distribution is affected by human acceptance, and better understand and predict expansion processes and recolonisation events. Wildlife and humans are increasingly sharing space, and wildlife management planning cannot ignore human attitude and activities. Our approach provides an effective method for accounting for the human and ecological aspects simultaneously, and can be used to develop evidence-based conservation planning, targeting both social and ecological components.

Authors' contributions

GC, DMB and AO conceived the study; GC and DMB designed the methodology; DMB collected and analysed the data; DMB, GC and AO interpreted the results; DMB wrote the first version of the manuscript and all authors contributed substantially to the revisions.

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Data accessibility

Questionnaire responses are available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.t4t73 (Behr, Ozgul & Cozzi 2017).

Data source of predictors used for a spatially explicit representation of human acceptance is indicated in Appendix S3.

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Table 1: Ascertained human-related wolf mortality in Switzerland between 1995 and 2015.

Legally shot		Poached		Collisions	
Canton	Year	Canton	Year	Canton	Year
VS[a]	2000	VS	1998	VS[c]	1999
VS	2000	GR	2014	BE[d]	2006
GR	2001	GR[b]	2014	TI[d]	2013
VS*	2002			ZH[d]	2014
VS*	2003				
VS	2006				
VS	2006				
VS	2009				
LU*	2009				
VS	2009				
VS	2010				
VS	2013				
VS*	2015				
VS*	2015				
UR*	2015				

Data from KORA: “Übersichtsliste aller in der Schweiz genetisch nachgewiesenen Wölfe seit 1998” and PRONATURA: “Geschichte der Rückkehr des Wolfes in die Schweiz”.
VS and BE: western Alps; LU and UR: central Alps; GR and TI eastern and southern Alps; ZH: Central Plateau.
*granted shooting license but wolf not found within allowed time window; [a] likely deadly injured but body not found. [b] mistaken for a fox; [c] snowplough; [d] train.

Table 2: Relation of human acceptance to socio-demographic parameters and factors included in final model (top row) using multiple linear regression analysis. The coefficient estimate and standard error from the final model are reported for each parameter, as is the effect of removing each parameter from the final model on the AIC (ΔAIC). The abbreviated explanatory variables are *livest.prot* = need for livestock protection, *hhsize* = size of household, *vac.home* = vacation home owner in mountains, *livest.owner* = livestock owner.

Dependent variable: human acceptance				
Model	estimate	std. error	p-value	ΔAIC
proximity + interest + fear + harmfulness + livest.prot + gender + age + children + hhsize + education + hunter + livest.owner + age:livest.owner + children:hhsize				0
- children(yes) (- children(yes):hhsize)	0.27	0.29	0.35	1.1
- hhsize (- children(yes):hhsize)	-0.09	0.22	0.69	1.3
- age:livest.owner(yes)	0.74	0.37	0.05	2.0
- children(yes):hhsize	-1.04	0.47	0.03	3.0
- gender(male)	-0.44	0.19	0.02	3.6
- livest.owner(yes)	-0.43	0.20	0.03	5.4
- education*				8.7
- proximity	-0.58	0.18	<0.001	9.0
- hunter(yes)	-1.21	0.33	<0.001	11.6
- age	-0.83	0.20	<0.001	17.8
- fear	-3.18	0.25	<0.001	155.3
- livest.prot	3.67	0.23	<0.001	235.2
- interest	3.14	0.20	<0.001	238.3
- harmfulness	-6.47	0.28	<0.001	471.7

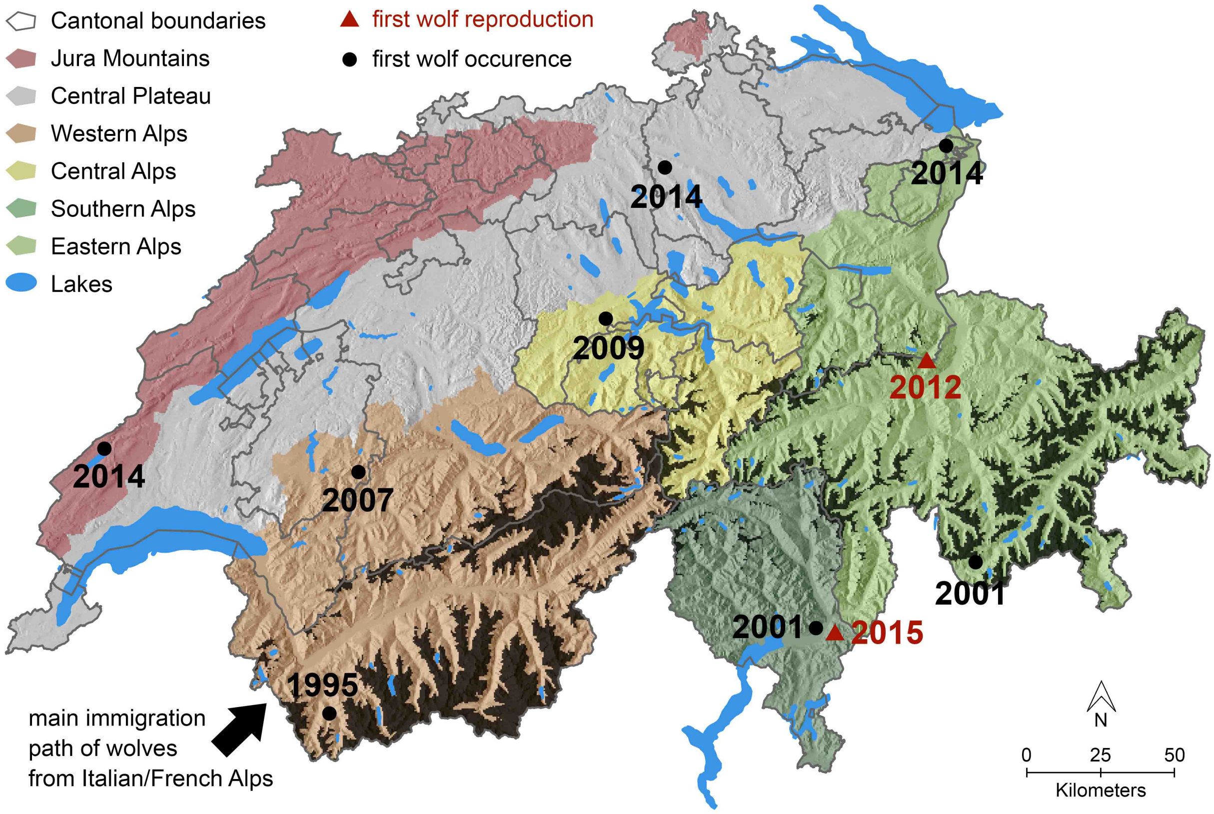
*categorical variable with more than two levels

Table 3: Relation of human acceptance to geo-referenced predictors included in final model (top row) using logistic regression analysis. The explanatory variables are *agricul* = agricultural areas, *elev* = mean elevation, *wolf* = wolf distance, *lang* = language, *dens* = human density, *age* = mean age, *livest* = small livestock, *autocov* = autocovariate.

Dependent variable: human acceptance				
Model	estimate	std. error	p-value	ΔAIC
agricul + elev + wolf + lang + dens + livest + tour + autocov + elev:livest + dens:livest + livest:tour				0
- autocov	-0.03	0.12	0.32	1.4
- agricul	-0.27	0.18	0.13	2.2
- lang*				3.8
- dens:livest	0.79	0.43	0.07	4.5
- wolf	0.27	0.12	0.03	4.6
- dens (-dens:livest)	0.39	0.18	0.03	4.7
- tour (-livest:tour)	0.29	0.15	0.06	4.8
- livest:tour	0.76	0.34	0.03	6.3
- elev:livest	-0.93	0.36	0.01	9.9
- livest (-dens:livest - livest:tour - elev:livest)	-0.16	0.13	0.23	25.6
- elev (-elev:livest)	-1.12	0.22	< 0.001	39.0

*categorical variable with more than two levels

Figure 1: Topographic map of Switzerland subdivided into Jura Mountains, Central Plateau and Alps. The Alps are in turn divided in four regions. Locations and dates of first confirmed wolf appearance (round symbols) and of first confirmed reproduction (triangles) in different regions are shown. Black shaded areas denote mountains >2500 m above sea level and may represent a natural expansion corridor from south-west (where wolves enter Switzerland) to north-east (where wolves reproduced in 2012 for the first time).



712 **Figure 2:** Raster representation of predictor variables used to model spatial distribution of
713 human acceptance (see text and Appendix S3 for further details).

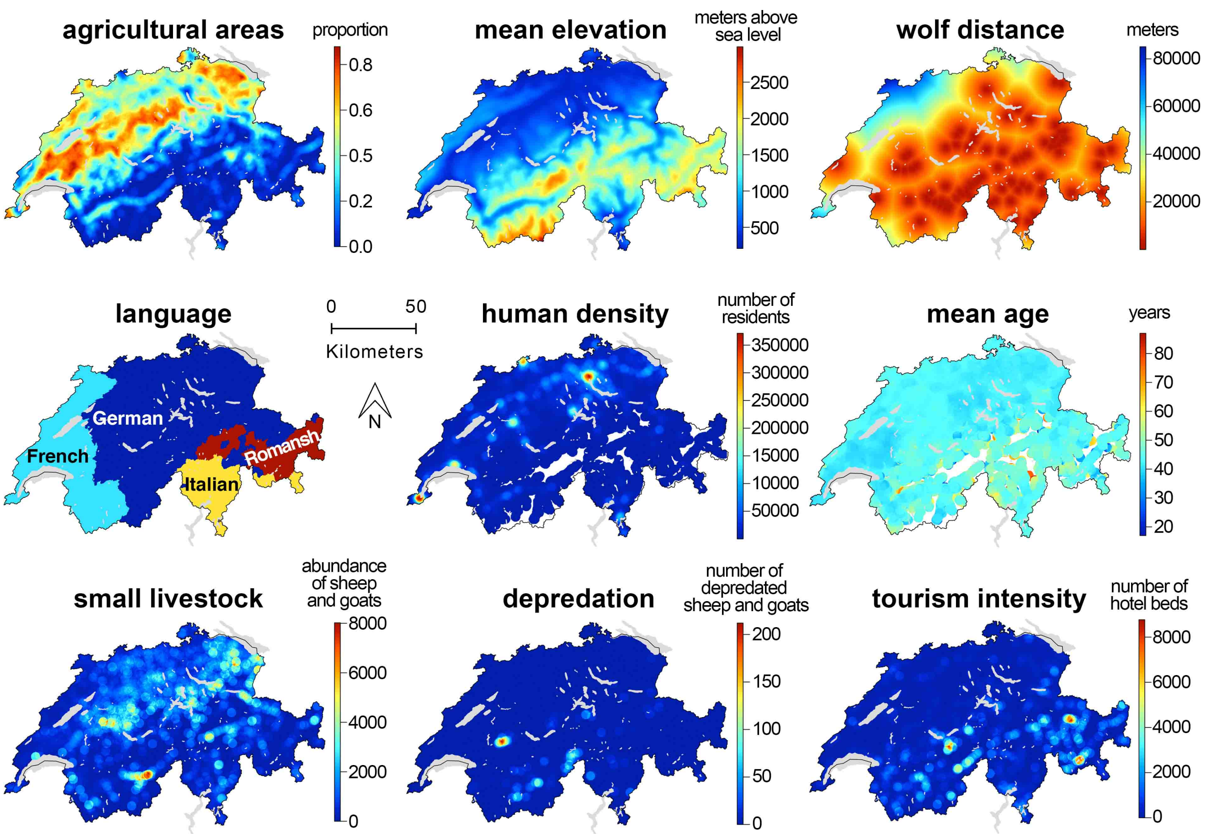


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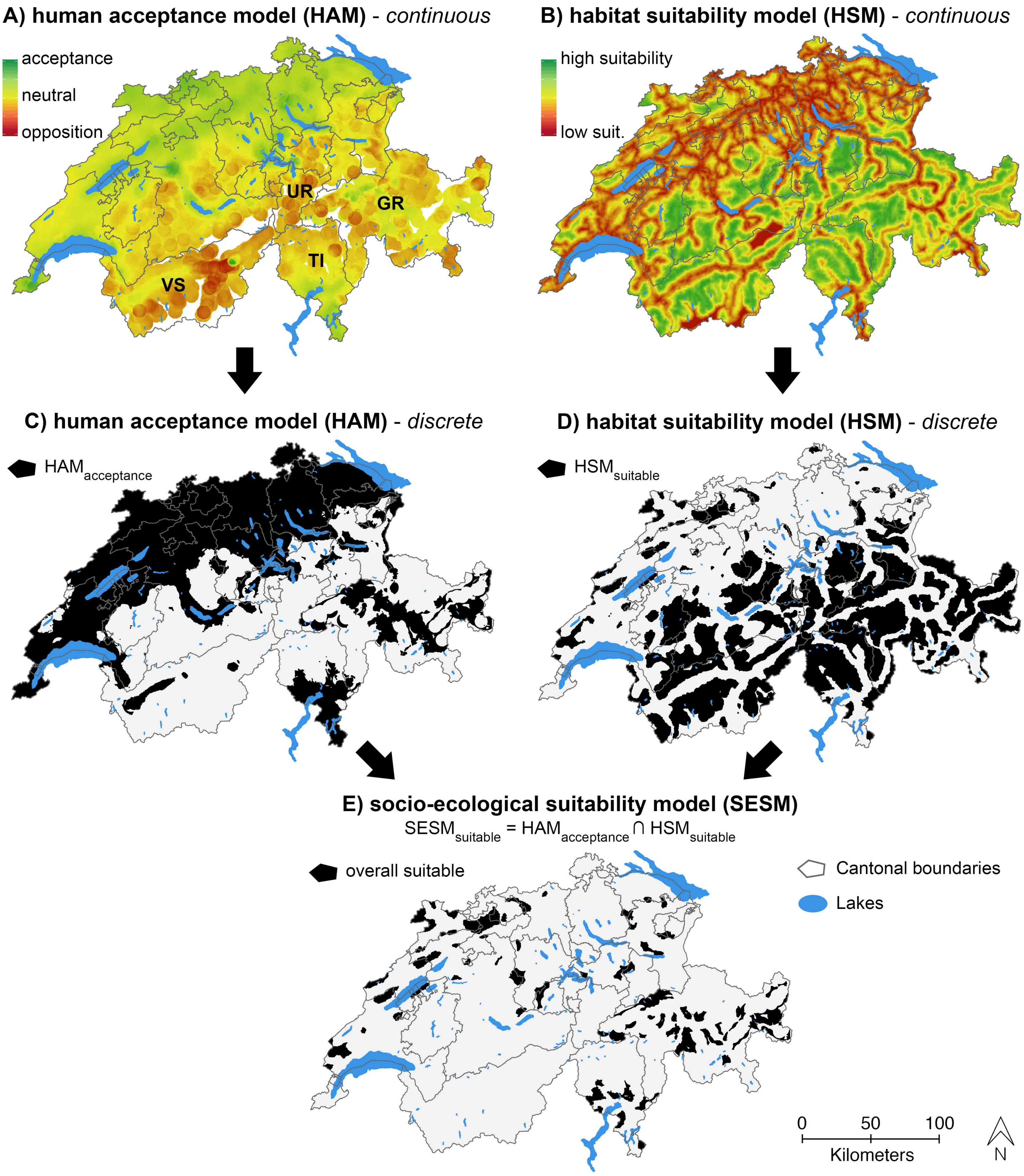
Figure 3: Spatially explicit human acceptance model (HAM), habitat suitability model (HSM), and socio-ecological suitability model (SESM) for the wolf in Switzerland (refer to main text for further details). VS: canton of Valais, UR: canton of Uri, TI: canton of Ticino, GR: canton of Graubünden.



Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Questionnaire used in the survey.

Appendix S2. Correlates of human acceptance.

Appendix S3. Predictors used for a spatially explicit representation of human acceptance.

Table S1. Determinants of perceived harmfulness of the wolf.

Table S2. Small livestock abundance and depredation by wolves.

Fig. S1. Consequences of change in human acceptance.